Relative contributions of soil, foliar, and woody tissue respiration to total ecosystem respiration in four pine forests of different ages

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[1] Carbon dioxide (CO_2) emissions from soil, foliage, and live woody tissue were measured throughout the year in afforested, white pine (*Pinus strobus* L.) stands (67, 32, 17, and 4 years old as of 2006), growing in a northern temperate climate. The data were used to estimate annual ecosystem respiration (*R*e) and its component fluxes, including soil, foliar, and woody tissue respiration; to investigate major environmental factors causing intersite and temporal variability in the observed fluxes; and to compare chamber-based *R*e estimates with eddy covariance-based estimates. While temperature was the dominant driving factor of temporal variability in component fluxes, intersite variability in CO_2 emissions was attributed to differences in stand physiological characteristics, such as the presence of the LFH soil horizon, its carbon-to-nitrogen ratio, and the amount of canopy cover. Additional factors that contributed to flux variability included the frequency of precipitation events, vapor pressure deficit and stem diameter, depending on the component considered. Estimated annual chamber-based totals of *R*e across the four stands were 1526 ± 137, 1278 ± 137, 1985 ± 293, and 773 ± 46 g C m^{-2} yr^{-1} for the 67-, 32-, 17-, and 4-year-old stands, respectively. Soil respiration dominated emissions at the 4-year-old stand, while foliar respiration dominated emissions at the 17-year-old stand. In contrast, at the two oldest stands, soil and foliar respirations were comparable. Soil respiration accounted for 44%, 44%, 26%, and 70% of annual *R*e, across the 67-, 32-, 17-, and 4-year-old stands, while foliar respiration accounted for 48%, 41%, 60%, and 30% of annual *R*e, across the respective sites. Wood respiration was the smallest component of annual *R*e across the stands (8%, 15%, 14%, and 0.1%, respectively). The chamber-based *R*e values were higher than tower-based eddy covariance *R*e estimates, on average by 18%, 70%, 18%, and 36% at the 67-, 32-, 17-, and 4-year-old stands, respectively. This study contributes to our general understanding of the age-related effects and the role of climate on carbon emissions from various components of afforested ecosystems. Our results suggest that foliar respiration could be comparable to or higher than soil respiration in its contribution to *R*e in young to mature, planted or afforested, ecosystems. They also suggest that site quality and stand age are important factors to be considered in future studies of carbon dynamics of afforested stands.

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1. Introduction

[2] Afforestation, planting forests on abandoned agricultural and marginal lands, has been proposed as a means to help sequester anthropogenic carbon emissions [*Nabuurs et al.*, 2007; *Intergovernmental Panel on Climate Change*, 2007]. On an annual basis, the net carbon balance of a forest ecosystem is determined by two major fluxes: uptake due to photosynthetic activity and emissions due to respiratory fluxes (*R*e). *Arain and Restrepo-Coupé* [2005] have shown that both fluxes are significantly higher for planted or afforested stands when compared to naturally regenerated forests, while others have shown that, of the two fluxes, *R*e

determines the sink/source strength of forest ecosystems [*Valentini et al.*, 2000; *Kolari et al.*, 2004]. Therefore, if afforestation is to be used for atmospheric carbon mitigation purposes, it is necessary to understand the carbon dynamics of afforested stands, including the factors that drive the variability of *R*e.

[3] In the past 20 years, there have been many studies that assess the carbon dynamics and sink/source potential of forest ecosystems based on carbon dioxide (CO_2) flux measurements (see review by *Baldocchi* [2008]). However, most of these studies focused on naturally regenerated stands or those planted after disturbances such as fire [*Hermle et al.*, 2010; *Amiro et al.*, 2006; *Bond-Lamberty et al.*, 2004] or harvest [*Zha et al.*, 2009; *Humphreys et al.*, 2006; *Kolari et al.*, 2004, *Law et al.*, 2003]. The carbon dynamics of these stands are expected to be quite different compared to those of afforested stands, especially during the initial years after establishment. For example, after a fire, there often remains a significant amount of aboveground biomass and dead root biomass, which could contribute to increased ecosystem respiration due to decomposition in the years that follow [*Amiro et al.*, 2006; *Bond-Lamberty et al.*, 2004, *Litvak et al.*, 2003]. Likewise, there may also be a significant amount of carbon left behind at a site after a forest harvest, in terms of logging residue, the LFH soil horizon, and dead roots, all of which can contribute to increased respiration, due to decomposition in the initial years after harvest [*Humphreys et al.*, 2006; *Kolari et al.*, 2004]. The presence of the LFH horizon and debris could moderate soil temperature and moisture dynamics [*Bond-Lamberty et al.*, 2004], preventing extremes in soil temperatures and moisture conditions that afforested sites may experience before canopy closure. Soils in afforested stands are likely to have depleted organic carbon in the initial years after establishment [*Hooker and Compton*, 2003; *Thuille and Schulze*, 2006]. They also may lack extensive belowground biomass accumulation prevalent on former forested or grassland sites. Variable nutrient contents of soils on former agricultural or marginal lands are also expected, which can in turn affect site quality and consequently the carbon dynamics of newly established stands.

[4] The study of *R*e dynamics is further complicated by the fact that *R*e is a sum of component fluxes that differ in their response to environmental factors, such as temperature and moisture [*Gaumont-Guay et al.*, 2006], and also to stand physiological characteristics, such as canopy cover, stand age, and nutrient contents [*Bolstad et al.*, 2004; *Vose and Ryan*, 2002]. On annual basis, the major components of *R*e include carbon emissions from soils (from roots and microorganisms), foliage, and woody tissue respiration. Several studies have investigated the variability in annual *R*e composition within various forest ecosystems [*Bolstad et al.*, 2004; *Gaumont-Guay et al.*, 2006; *Lavigne et al.*, 1997; *Law et al.*, 1999; *Tang et al.*, 2008; *Vose and Ryan*, 2002], but only two studies were of young to mature (0- to 70-year-old) planted forests in temperate climates [*Bolstad et al.*, 2004 and *Vose and Ryan*, 2002], where afforestation since the 1950s is believed to have led to increased carbon sequestration [*Van Minnen et al.*, 2009]. A young, recently established stand will be expected to have lower accumulated biomass and carbon stocks compared to a mature stand [*Hooker and Compton*, 2003], which in turn will impact *R*e composition and dynamics. For example, *Tang et al.* [2008] found that *R*e generally increased from young to mature forests and then declined from mature to old-growth stands. Young stands with open canopies have been shown to respire less compared to older stands [*Lindroth et al.*, 2008; *Noormets et al.*, 2007]. However, young stands may be growing more actively and so their growth and maintenance respiration may be higher than those of mature stands. Therefore, in addition to land use history, the age-related variability in forest carbon dynamics should also be considered in studies of afforested stands.

[5] Several techniques can be used to estimate *R*e in forests, with the most widely used one being the eddy covariance technique [*Baldocchi*, 2003]. *R*e can also be estimated as a sum of chamber-based measurements of various respiratory components that have been scaled-up to the ecosystem level [*Gaumont-Guay et al.*, 2006; *Lavigne et al.*, 1997; *Law et al.*, 1999; *Tang et al.*, 2008]. *R*e estimates using the eddy covariance technique are generally lower than chamber-based estimates, with differences ranging from 2% to 63% [*Gaumont-Guay et al.*, 2006; *Lavigne et al.*, 1997; *Law et al.*, 1999; *Tang et al.*, 2008]. Chamber methods have an advantage over the eddy covariance technique, because of their ability to partition CO_2 emissions into various ecosystem components, such as soil, foliage, and woody tissue respiration. This, in turn, can allow researchers to determine the contribution of each component flux to the overall ecosystem respiration and improve our understanding of *R*e dynamics.

[6] The objectives of this study were (1) to investigate the driving factors of intersite and temporal variability of soil, foliage, and live woody tissue respiration across four afforested stands of different ages; (2) to quantify and compare the contribution of each respiration component to total ecosystem respiration; and (3) to compare total ecosystem respiration derived from scaled-up chamber measurements with that derived from eddy covariance measurements at the sites.

2. Methods

2.1. Study Sites

[7] This study was conducted at the Turkey Point Flux Station (TPFS), located on the north-western shore of Lake Erie, in southern Ontario, Canada. TPFS consists of an age sequence of four white pine (*Pinus strobus* L.) stands, which were 4, 17, 32, and 67 years old at the time of the study in 2006. The 67- and 32-year-old sites are located beside each other, whereas the 17-year-old and 4-year-old sites are located about 10 km northwest and 18 km west of the two older sites, respectively. The two oldest stands (67 and 32 years old) were planted, or afforested, to stabilize local sandy soils, while the two younger stands (17 and 4 years old) were planted on abandoned agricultural lands that were last cultivated 10 years prior to tree planting. In 1983, thinning was performed at the 67-year-old site, during which 104.76 m^3 ha^{-1} of wood volume was removed from a 38.6 ha area (Ontario Ministry of Natural Resources records). The remaining sites have not been thinned yet. Further stand characteristics are given in Table 1. Hereafter, we refer to the four sites by their shortened code names: TP39, TP74, TP89, and TP02. The acronyms correspond to "Turkey Point", followed by stand establishment year, i.e. 1939, 1974, 1989, and 2002, respectively.

Table 1. Site Characteristics[a]

Site Characteristic	TP39	TP74	TP89	TP02
Location	42°42′55″N 80°22′20″W	42°42′34″N 80°21′05″W	42°46′32″N 80°28′28″W	42°39′49″N 80°34′24″W
Elevation (m)	184	184	212	265
Maximum LAI (m^2/m^2)[b]	8.0	5.9	12.8	N/A
Mean annual LAI (m^2/m^2)[c]	4.6	3.4	7.4	0.9
Tree height (m)[d]	20.2	11.2	9.1	0.94
DBH (cm)[d]	34.6	15.6	15.8	N/A
Stem density (trees/ha)[d]	429 ± 166	1492 ± 322	1242 ± 263	1683 ± 147
Stem volume (m^3/ha)[d]	376	160	116	0.45
Live branch volume (m^3/ha)	58	72	101	N/A
Total sapwood volume (m^3/ha)[e]	178	170	176	0.45
Foliar biomass (kg/ha)[d]	2855	4601	8727	208
Foliar N (mg/g)[f]	13.9	11.3	13.4	21.4
Foliar CN[f]	38.2	46.2	39.1	34.8
Litter-fall[d,g] (kg/ha, Sept-Nov)	1725	1864	3698	N/A
Litter-fall[d,h] (kg/ha, total annual)	3990	2980	5190	N/A
Litter thickness (cm)	4.13 ± 1.09	3.63 ± 0.80	4.11 ± 1.27	0
Litter CN ratio	17.4 ± 4.8	24.5 ± 5.6	16.1 ± 7.1	N/A
Mineral soil carbon (top 55 cm)[d]	36.7	30.1	33.9	37.2
Mineral soil available P (ppm)[i]	139 ± 18	117 ± 21	188 ± 56	169 ± 82
Mineral soil Mg (ppm)[i]	10 ± 3	13 ± 6	33 ± 34	44 ± 5
Mineral soil K (ppm)[i]	12 ± 5	10 ± 3	32 ± 18	48 ± 18
Mineral soil Ca (ppm)[i]	109 ± 28	153 ± 107	827 ± 994	1669 ± 753

[a]N/A, measurement unavailable.
[b]From *Chen et al.* [2006], measured in August 2005.
[c]Estimated from our seasonal measurements with LI-2000, not corrected for clumping.
[d]Mean values from *Peichl and Arain* [2006]; where applicable, data are for trees with diameter at breast height (1.3 m), DBH > 9 cm.
[e]Estimated (i.e., sum of stem and branch sapwood volume, assuming branches are 100% sapwood).
[f]Measured by Larry Flanagan, University of Lethbridge, AB (unpublished).
[g]Includes only white pine needles.
[h]Includes needles, leaves, and cones.
[i]Nutrients measured in the top 20 cm of the mineral soil (P, phosphorus; Mg, magnesium; K, potassium; Ca, calcium).

[8] All four stands grow on well-drained sandy soils, classified as Brunisolic Gray Brown Luvisols, following the Canadian Soil Classification Scheme [*Presant and Acton*, 1984]. The climate in the region is cool temperate. On the basis of a 30-year record, from a World Meteorological Organization-accredited Environment Canada station, located 10 km north of the youngest site at Delhi, Ontario, the mean annual air temperature is 7.8°C, and mean annual precipitation is 1010 mm at TPFS [*Environment Canada*, 2008]. Normally, the precipitation is distributed evenly throughout the year, with 133 mm falling as snow. At the time of the study, TP39 had a well-developed understory of white pine seedlings (*Pinus strobus* L.), black cherry (*Prunus serotina* Ehrh.), white oak (*Quercus alba* L.), poison ivy (*Rhus radicans* L. ssp.), bracken ferns (*Pteridium aquilinum* L.), and blackberry (*Rubus allegheniensis* Porter). TP74 had minimal understory vegetation, patches of moss cover consisting mostly of *Polytrichum spp*., and occasional fungi. TP89 had no understory growth, only a layer of pine needles and occasional fungi. The youngest stand (TP02) had no effective litter layer accumulation. Seasonal herbaceous growth (grasses, weeds, etc.) occurred at TP02 from May to October. Further site characteristics are given in the study by *Peichl and Arain* [2006] and *Peichl et al.* [2010], but relevant site characteristics are also given in Table 1.

2.2. Eddy Covariance-Based Ecosystem Respiration and Meteorological Measurements

[9] Net ecosystem exchange (NEE) was measured at each site using the eddy covariance (EC) technique. At TP39, a permanent closed-path EC system has been operating since 2002, on top of a 28 m walk-up tower. For details regarding the closed-path EC system set-up, see *Arain and Restrepo-Coupé* [2005]. A roving open-path EC system was used to measure NEE at the three younger stands. The open-path system was rotated among the three younger sites on biweekly to monthly time intervals, from 2004 to 2006 [*Peichl et al.*, 2010]. Meteorological and flux data were quality controlled following Fluxnet-Canada Research Network protocols. Further details of eddy covariance systems and flux and meteorological data analysis are given in *Peichl et al.* [2010].

[10] In brief, eddy covariance *R*e (*R*e _ec) was calculated using a nonlinear logistic relationship between nighttime NEE, when site-specific friction velocity (u^*) was above its minimum threshold value (i.e., 0.325, 0.15, 0.1, and 0.1 m s^{-1} for the 67-, 32-, 17-, and 4-year-old sites, respectively) and soil temperature at 5 cm depth [*Arain and Restrepo-Coupé*, 2005]. The *R*e_ec versus soil temperature (*T*s) relationship was calculated for each individual year at TP39, whereas at the three younger stands, NEE data were pooled for 2003–2007 to fit a single relationship because of large gaps in measured EC fluxes at these sites. An analysis of flux data at TP39 showed that, over the 5-year study, the difference between annual *R*e_ec derived from data pooled over 2003–2007 versus *R*e_ec derived for individual years was less than 5% [*Peichl et al.*, 2010]. Missing nighttime NEE values (i.e., *R*e_ec) were filled using this relationship.

[11] Meteorological variables such as radiation, air temperature, humidity, wind speed, and direction, etc., were

measured using automatic weather stations at all four sites throughout the year. Additionally, at TP39, precipitation was measured using a heated tipping bucket rain gauge mounted above the canopy, on the flux tower. The four sites experienced similar climate. For example, mean daily above-canopy air temperature (*T*air) measurements across all four sites were comparable (for a 1:1 linear relationship, using *T*air observations from 2003 to 2006; coefficient of determination, $R^2 = 0.995$, 0.995, 0.993; and slopes = 1.010, 1.004, and 1.005 for TP74, TP89, and TP02, respectively; plots not shown). Therefore, the mean daily and annual climatic variables presented below are those from the TP39 site because this site had the most continuous record of all four sites.

[12] At each site, soil temperature was continuously measured at two locations at 2, 5, 10, 20, 50, and 100 cm depths. Similarly, volumetric soil water content (cm^3 cm^{-3}) was measured at the same two locations at 5, 10, 20, 50, and 100 cm depths at the three oldest stands, and at 5, 10, 20, and 50 cm depths at TP02 using water content reflectometers (CS615; Campbell Scientific Inc.). Meteorological and soil data were recorded at half-hour intervals. See further details on meteorological measurements in the study by *Peichl et al.* [2010].

2.3. Chamber-Based Ecosystem Respiration and Its Component Measurements

2.3.1. Soil Respiration

[13] Soil respiration (*R*s) was measured on a monthly basis from 1 January 2006 to 31 December 2006, along 50 m transects, using a portable chamber system, the LI-6400 photosynthesis system (LI-COR Inc., NE, USA) that had a soil chamber and a 15 cm soil temperature probe attachments (models LI-COR 6400-09 and LI-COR 6400-013, respectively; LI-COR, Inc., Lincoln, NE, USA). In 2003, 12 PVC collars (10.16 cm in diameter, 7.5 cm long, inserted into the soil to a depth of about 5 cm) were installed at 4 m intervals along each transect, as part of a long-term study (2003–2006). Once installed, collars remained in the ground for the duration of the study. Herbaceous vegetation inside collars was avoided during initial installation. Any vegetation that grew up inside any collar, since installation, was trimmed back to the soil surface.

[14] At each sampling point, three replicate *R*s measurements were recorded. At the same time, soil temperature ($Ts_{\_LI\_COR}$) was also measured, within 20–30 cm of each collar, using the LI-COR temperature probe inserted vertically to its full length. The probe was not used during winter, when the top of the soil was frozen. In modeling analysis as described below, missing winter $Ts_{\_LI\_COR}$ measurements (3% of total) were supplemented with soil temperature measurements from each site′s weather station. Soil temperature from the LI_COR probe (at 15 cm depth) and the weather station′s soil temperature probes (within top 20 cm of soil surface) were comparable within 2% across all four sites (R^2 = 0.99–0.98, data not shown).

[15] Measuring *R*s over snowpack is a challenge [*McDowell et al.*, 2000]. At TPFS, snow accumulation was sporadic throughout the winter. During our study, when large snow accumulations completely covered our permanent collars along transects, *R*s measurements were made directly over snow, in the vicinity of the permanent collars, using a custom-made snow collar. This snow collar was simply one of our PVC collars, as described above, mounted onto a square, framed, metal mesh, which created a "snow-shoe" that prevented the collar from sinking into the snow once the chamber was set on it. The PVC collar was mounted halfway into the mesh. During measurements, the collar was gently inserted into the deep snow few minutes before the Li-6400 chamber was placed over it. This allowed for any flux of CO_2 due to snowpack disturbance to vent off, before the chamber was placed over the collar. However, due to the possibility of horizontal advection of CO_2 in the snowpack during measurements, because the PVC collar did not go down all the way to the ground when inserted, we did not use these observations in model parameterization. Overall, during 2006, only 1 out of the 5 days of winter measurements had enough snow accumulation to require the use of the snow collar. This measurement was excluded from model analysis below but is still shown in the figures as part of the observations.

2.3.2. Foliar Respiration

[16] Because of logistic constraints, we were unable to measure foliar respiration (*R*f) during nighttime. However, we used dark foliar gas exchange measurements collected across TPFS as part of controlled light response curve measurements conducted in a separate photosynthesis study. Thus, *R*f is defined here as net CO_2 exchange of foliage at zero light level (i.e., photosynthetically active radiation, PAR = 0 μmol m^{-2} s^{-1}). The LI-6400 instrument was used to generate the light response curves, using the 2 × 3 cm^2 foliar chamber attachment (LI-COR Inc., NE, USA). An artificial light source attachment, 6200-02B LED and the 6400-01 CO_2 mixer were used to control chamber light and CO_2 conditions, respectively. Light response curves were measured under controlled chamber conditions: fixed air temperature, which was within 5°C of ambient temperature; CO_2 concentration between 360 and 380 ppm; and changing chamber light conditions (i.e., stepwise reduction of PAR from saturation at 2000 to 0 μmol m^{-2} s^{-1}). For this study, only measurements corresponding to net gas exchange measurements at PAR = 0 μmol m^{-2} s^{-1} were used. In each case the measured foliage was slowly acclimatized to low light (at least half an hour) before being subjected to complete darkness for the *R*f measurement. During the low to zero PAR measurements (i.e., 200 to 0 μmol m^{-2} s^{-1}), the foliage surrounding the chamber was also covered with a nontransparent cloth, to reduce light levels to the surrounding foliage on the measured branch, not just the needles in the chamber.

[17] Ten to fifteen white pine needles (2–3 whorls) were placed in a single flat layer into the chamber, such that the length of the needles inside the chamber was 3 cm. Chamber area was set to 1 cm^2 in the instrument program that recorded the measurements. Later the measurements were corrected for the so called true half-surface area (HSA) of the needles in the chamber, which represented an estimate of the surface area of needles exposed to the light source in the chamber. The true HSA was determined using the volume displacement method described by *Brand* [1987]. Corrected respiration measurements were used for *R*f model parameterization.

[18] Two trees were sampled at TP39 by accessing their middle canopy from the eddy covariance walk-up scaf-

folding tower. At TP74 and TP89, three trees were sampled at midcanopy, using scaffoldings to reach the midcanopy of the trees. At TP02, the trees were small enough to be accessed at midcanopy from the ground. Measurements were conducted on 1-year-old needles. One light response curve was measured at each of the sampled trees at each site, on a monthly basis from June to August in 2006, and *R*f was extracted from each curve. Additional light-response curves were conducted at TP39 and TP02 in April, May, September, and November in 2007 to capture seasonal variability in foliar fluxes. Interannual variability in *R*f was assumed to be small compared to seasonal and intersite variability of respiration across these different-age stands.

2.3.3. Woody Tissue Respiration

[19] We used the approach of *Xu et al.* [2000] to measure woody tissue respiration (*R*w) at the three older stands, using the LI-6400 system with its soil chamber attachment. In autumn of 2005, four trees of variable diameter were selected around the EC towers at each stand. Collars (same make and diameter as those used for soil respiration) were attached vertically at 1.3 m height on the stem of each tree with silicone, following *Xu et al.* [2000]. Loose bark was removed around the circumference of the collar, as necessary. Woody tissue respiration was sampled on a monthly basis, from April to November 2006. At the end of the measurement campaign, increment cores were taken from the center of each collar to determine the sapwood volume under the collars as follows: the area enclosed by the collar (i.e., πr^2, where r was the radius of the collar on the stem) was multiplied by the width of sapwood below the collar, which was measured from the tree core taken from the center of the collar. Measured respiration values were corrected from per surface area to per sapwood volume before being used in model parameterization.

[20] At the two oldest stands, tree bole temperature (*T*b) was measured in several trees using thermocouples that were continuously sampled, every half hour, by the weather station data logger. These thermocouples were inserted into sapwood at 2–5 cm from the surface. Missing *T*b values and those for TP89 were estimated from air temperature (*T*a), separately for each site, using linear regressions developed between *T*a and *T*b at TP39 and TP74. For model parameterization, *T*b values corresponding to the time of day when *R*w was measured were used.

[21] At TP02, because of the small size of the tree stems, we were unable to implement our *R*w chambers to measure *R*w directly. However, we estimated *R*w for TP02 by assuming that the rate of woody tissue respiration would be similar to that of the second youngest stand (TP89). Thus, we used simulated *R*w values from TP89, upscaled them with an estimate of sapwood volume per square meter at TP02. Past biomass studies at TP02 showed that the wood in the seedlings was all sapwood because of the young age and tree size of the stand at the time of this study [*Peichl and Arain*, 2007].

2.4. Data Analysis

[22] We used the Gamma model [*Khomik et al.*, 2009] to simulate component fluxes at our sites:

$$R_i = T_i^{\alpha} e^{\beta_0 + \beta_1 T_i}, \quad (1)$$

where R_i is respiration of component i in μmol of CO_2 m^{-2} s^{-1}; T_i is the temperature of component i in °C, but shifted by 40°C (i.e., T_i = measured temperature + 40°C, see *Khomik et al.* [2009] for more details); and α, β_0, and β_1 are the model parameter coefficients to be estimated. The model was linearized before being parameterized, by taking the natural logarithm of equation 1.

[23] To investigate intersite differences in fluxes, the model was parameterized, individually, for each component using all observations, with the exception of one snow-covered day described above. Intersite differences were initially tested using the categorical variable (i.e., "dummy variables") approach [*McClave and Sincich*, 2003, p. 630]. This allowed the α, β_0, and β_1 (equation 1) to vary among sites of different ages, as follows:

$$\beta_0 = \beta_{01} + \beta_{02}\mathrm{A2}_i + \beta_{03}\mathrm{A3}_i + \beta_{04}\mathrm{A4}_i, \quad (2a)$$

$$\beta_1 = \beta_{11}\mathrm{T}_i + \beta_{12}\mathrm{A2}_i\mathrm{T}_i + \beta_{13}\mathrm{A3}_i\mathrm{T}_i + \beta_{14}\mathrm{A4}_i\mathrm{T}_i, \text{and} \quad (2b)$$

$$\alpha = \alpha_1\mathrm{LnT}_i + \alpha_2\mathrm{A2}_i\mathrm{LnT}_i + \alpha_3\mathrm{A3}_i\mathrm{LnT}_i + \alpha_4\mathrm{A4}_i\mathrm{LnT}_i, \quad (2c)$$

where β_{01}, β_{02}, β_{03}, β_{04}, β_{11}, β_{12}, β_{13}, β_{14}, α_1, α_2, α_3, and α_4 are unknown coefficients to be estimated. In equations 2b and 2c, the terms involving the product of a dummy variable and T_i or $\mathrm{Ln}T_i$ are called "interaction terms. " By considering the product of a dummy variable and T_i as a new explanatory variable, equation 1 is transformed into a multivariate linear regression model [*Otomo and Liaw*, 2003]. In this model, all of the unknown coefficients can be simultaneously estimated by using a linear regression procedure in any widely available statistical software, such as SAS (SAS Institute Inc., NC, USA) or SPSS (SPSS Inc., IL, USA).

[24] To establish which environmental factors other than temperature controlled variability in *R*e components, we tested the following additional explanatory factors in our models: the thickness of the LFH soil horizon (LFH) and its carbon-to-nitrogen ratio (CN), soil volumetric water content, air temperature, precipitation amount and frequency, photosynthetically active radiation, stem diameter, and vapor pressure deficit. These additional variables, depending on the respiration component considered, were added into the linearized form of the Gamma model (equation 1) to create a multivariable linear regression model:

$$\mathrm{Ln}R_i = \alpha\mathrm{Ln}T_i + \beta_0 + \beta_1 T_i + \beta_2 X_2 + \ldots + \beta_n X_n, \quad (3)$$

where R_i, T_i, α, β_0, and β_1 are as in equation 1 above, X_2–X_n are additional explanatory variables and β_2–β_n are their corresponding model parameter coefficients to be estimated.

[25] The expanded models were evaluated, to determine which of the added variables were statistically significant in improving the model′s explanatory power (i.e., $P < 0.05$ of their estimated coefficient). Only variables that were statistically significant were retained in the final models (Table 2).

[26] During analysis, we observed that some of the environmental explanatory variables were able to replace the dummy variables representing intersite variability. This occurred if the two variables mutually excluded each other when both were included in the model simultaneously. Such

Table 2. Models Used to Simulate Respiration of Individual Component Fluxes, Including the Models′ Coefficient of Determination and the Number of Observations Used for Model Parameterization[a]

Component	Model	T-only R^2	R^2	n
Rs	$Rs = T_s^{\alpha}\, e^{\beta_{01} + \beta_1 Ts + \beta_{02}A_3 + \beta_2 Ta + \beta_3 PPT_{f\_1} + \beta_4 LFH + \beta_5 CN}$	0.85	0.88	1967
Rw	$Rw = T_b^{\alpha}\, e^{\beta_{01} + \beta_1 T_b + \beta_{02}A_2 + \beta_{03}A_3 + \beta_2 PPT_f + \beta_3 DBH}$	0.66	0.82	336
Rf	$Rf = T_a^{\alpha}\, e^{\beta_{01} + \beta_{11}T_a + \beta_{02}A_3 + \beta_{03}A_4 + \beta_{12}A_4T_a + \beta_2 VPD + \beta_3 PAR + \beta_4 PPT_{f\_1}}$	0.44	0.61	719

[a]Here, Rs is soil respiration (μmol CO_2 m^{-2} s^{-1}); Rw is woody tissue respiration of sapwood (μmol CO_2 $m^{-3}s^{-1}$); Rf is foliar respiration (μmol CO_2 m^{-2} s^{-1}; half-surface area, HSA); A_3, A_4 are categorical variables used to represent intersite variability (i.e., $A_3 = 1$ for all observations belonging to TP89 and zero otherwise, whereas $A_4 = 1$ for all observations belonging to TP02 and zero otherwise); PPT_f and PPT_{f_1} are categorical variables that represent the frequency of precipitation occurrence on the day of Rf measurement and 1 day before Rf measurement, respectively; LFH is site mean thickness of the LFH horizon (cm); CN is site mean carbon-to-nitrogen (CN) ratio of the LFH; Ta is air temperature (above canopy, °C); Tb is tree bole temperature (2–5 cm, °C); Ts is soil temperature (2–20 cm, °C); VPD is vapor pressure deficit; and α, β_x and β_{xx} are model parameters to be estimated (see Table 3 for values).

instances provided insight into which physiological factors influenced intersite variability in respiration.

[27] Statistical analysis and model parameterization was performed using the SAS 9.1 software. The unknown parameter coefficients were estimated using the linear regression procedure, PROC REG, in the SAS software.

[28] The best specification of the model for each component respiration was used to simulate the component CO_2 emissions on a daily timescale, using daily means and totals of meteorological variables as inputs. These values were then upscaled to the stand level, using biometric variables, and used to compute monthly and annual CO_2 emissions of Re components. In turn, Re values were simulated as the sum of daily Rf, Rs, and Rw values:

$$\text{daily } Re = \text{daily } Rf + \text{daily } Rw + \text{daily } Rs. \quad (4)$$

Monthly and annual Re values were computed from the sum of the daily Re values.

[29] Uncertainty in simulated component respiration fluxes were estimated as the ratio between ±2 standard deviations (σ_r) about the predicted value and the total annual predicted flux (i.e., $(2\sigma_r)/Ri$, where Ri was the annual predicted sum of the component i). The σ_r values were computed as $\sigma_r = 2\sqrt{n\sigma_s^2}$, where n is the sample size (i.e., 365 days of the year) and σ_r^2 is the error mean square from the model output. Both values used to compute the ratio were in their original simulated units prior to upscaling. This ratio was then applied to upscaled sums of the individual foliar and woody tissue fluxes to obtain an estimate of the error on those values. This was done since for Rf and Rw fluxes, the error computed from simulated values was not directly transferable to upscaled values as in the case of Rs measurements that were already in units of square meter per ground area. We also report uncertainty in Re, which we calculated arithmetically from Rs, Rw, and Rf uncertainties (i.e., as square root of the sum of squared uncertainties of the individual Re components, for a given time period).

2.5. Up-Scaling to Ecosystem Level

[30] Because simulated Rw were in units of per sapwood volume and simulated Rf in units of per half-needle-surface area (HSA), we upscaled them to per ground surface area of the stand, using biometric indices from the individual stands in order to compare them with associated Rs values and to calculate Re values (g m^{-2}).

[31] Foliar respiration was upscaled using seasonal leaf area indices (LAIs) for each site. Seasonal LAI for each site was determined using a combination of LAI measurements conducted by *Chen et al.* [2006] and our own seasonal measurements. *Chen et al.* [2006] reported LAI values for the three oldest stands that they measured once, in August 2005, using two different techniques (Li-2000 (Li-COR Inc. Lincoln, NE, USA) and TRAC (ThirdWave Engineering, Ottawa, Canada)). However, *Vose and Swank* [1990] reported that LAI in *Pinus strobus* L. forests varies considerably during the year, with peak LAI reported in late July for their site. Therefore, the LAI values presented in the study by *Chen et al.* [2006] were likely the maximum annual values for our sites. In order to determine the seasonal variation in LAI values, we used our own LAI measurements made during different seasons throughout the year at the sites, using the Li-2000. We determined the percent-relative contribution of these seasonal LAI values (i.e., spring, summer, and autumn of 2002) to that of the maximum LAI we measured at the end of the summer 2002. We then used these relative percent ratios to determine seasonal LAI values from the single measurement reported by *Chen et al.* [2006] for each site. We assumed Chen et al.'s measurements to be the more accurate estimates of the maximum seasonal LAI, compared to our measurements, because *Chen et al.* [2006] corrected their measurements for branch and needle clumping. No measurements of LAI for TP02 were available from *Chen et al.* [2006]; therefore for that site, we report our own estimates from the Li-2000 measurements (Table 1). We also assumed little interannual variability in LAI from years 2002 to 2006 in our estimates. These estimated seasonal LAI values were used to upscale modeled Rf (from g m^{-2} HSA per day) to per ground area (i.e., g CO_2 m^{-2} ground area) for each site by multiplying simulated daily Rf values by the corresponding seasonal LAI value (i.e., we estimated one mean LAI value for each month of the year).

[32] Rf was measured on 1-year-old foliage. We assumed that respiration from 1-year-old foliage was a good approximation of the overall mean canopy respiration at our sites. In white pines, most foliage is shed at the end of its second growing season, but a small fraction of foliage survives for up to 4 years [*Vose and Swank*, 1990]. At our sites, we mostly observed 0- to 2-year-old needles. Our Rf measurements were conducted at midcanopy. Differences in Rf are expected along the vertical profile of the tree canopy because of the variable gas exchange dynamics of sunlit and shaded foliage [*Givnish*, 1988]. Because of logistical constraints, we were able to sample only at midcanopy. Our upscaled measurements could over- or underestimate total

foliar gas exchange. However, we would like to point out that older white pine stands tend to have most of their needles on branches located several meters above the ground, at the top of the stem. Therefore, we assumed midcanopy measurements to be good representatives of overall canopy *R*f.

2.6. Upscaling *R*w to Stand Level

[33] Woody tissue respiration (simulated on per sapwood volume basis) was upscaled using mean stem sapwood volume per ground area of each stand. Sapwood volume was determined from a separate destructive sampling study at our sites [*Peichl and Arain*, 2007]. Branch sapwood volume was estimated by assuming branches were 100% sapwood and using branch volume per stand as determined by *Peichl and Arain* [2007]. Similarly, at TP02, the seedling trees were assumed to be 100% sapwood. One would expect *R*w values, which have been upscaled to the stand level, to vary due to differences in stem density, while *R*w values on per-sapwood-volume basis may also be affected by site quality, stand age, and thinning practices. Therefore, in our comparison of woody tissue respiration among TPFS sites, *R*w rates on per-sapwood-volume basis were used.

3. Results

3.1. Meteorology and Site Microclimate During the Study Year

[34] The study year 2006 was relatively warm and wet, compared to the 30-year norm for the area (Figures 1a and 1d). Mean annual temperature was 1.9°C above the norm (about 25% higher), and total annual precipitation was 177 mm above the norm (about 18% higher). Precipitation during normal years is usually evenly distributed throughout the year in the region. However, in 2006, higher precipitation occurred in winter (February) and later around September (Figure 1d). The seasonal course of soil temperature (*T*s) followed that of the mean daily air temperature with some lag (Figures 1a and 1b). Differences in soil temperature between sites were more pronounced than differences in soil moisture, with the youngest stand reaching some of the highest observed soil temperatures across all four sites (Figure 1b). Soil moisture (θs) at all four sites was relatively low, averaging about 0.12 cm^3 cm^{-3} per year, despite increased precipitation during the study year (Figure 1c). This was due to the sandy, well-drained nature of the soils at the sites. The annual ranges in θs were lower (0.14, 0.14, 0.12, and 0.10 cm^3 cm^{-3} for TP39, TP74, TP89, and TP02, respectively) than the annual ranges in *T*s (24.1°C, 26.0°C, 21.2°C, and 30.7°C, respectively).

3.2. Environmental and Physiological Controls on Respiration

3.2.1. Effect of Climate

[35] Multivariate analysis of observed data showed that temporal variability in temperature (i.e., soil temperature for *R*s, tree bole temperature for *R*w, and air temperature for *R*f) was the dominant driving factor of temporal variability of the respective component fluxes and consequently *R*e (Table 3). Temperature-only component models had R^2 vlaues of 0.85, 0.44, and 0.66 for *R*s, *R*f, and *R*w, respectively.

[36] However, several additional factors were found to be statistically significant ($P < 0.05$) in explaining *R*s variability: the thickness of the LHF horizon (LFH) and its carbon-to-nitrogen (CN) ratio, which accounted for intersite variability as discussed below; mean daily air temperature (*T*a); and precipitation frequency (represented by categorical variables, PPT_f and PPT_{f_1}) (Table 2). Including these additional variables in the *R*s model helped to improve the model′s R^2 (from 0.85 to 0.88). Daily soil moisture (i.e., daily mean of measurements in the top 20 cm of the mineral soil) was also tested in the *R*s model but was found to be insignificant ($P > 0.05$). However, moisture in the LFH horizon, which was not measured directly at TPFS, may have been more important to *R*s variability across our sites, compared to the mineral soil moisture content. The LFH and PPT_f variables were both found to be statistically significant in the model, with PPT_f becoming more significant once LFH was included in the model (results not shown).

[37] The *R*f model was first parameterized with observed *R*f values and the estimated foliar temperatures, measured within the chamber. The model produced R^2 of 0.44 (adjusted $R^2 = 0.44$). However, because we did not have continuous measurements of foliar temperature at the sites to simulate daily *R*f, we assumed that *T*a was a good surrogate temperature for *R*f. Therefore, we also fitted the model to observed *R*f values and the corresponding mean daily *T*a at each site and found that the fit with *T*a was as good as with foliar temperatures (R^2 remained 0.44). Additional variables that helped to explain *R*f variability in the model included stand age, mean daily vapor pressure deficit (VPD), mean daily downwelling photosynthetically active radiation, and the frequency of precipitation 1 day before *R*f measurements (Table 2). Including those variables in the model improved its explanatory power by 17% ($R^2 = 0.61$). Of the additional variables, VPD was found to be negatively related to *R*f.

[38] The additional variables that improved the *R*w model′s explanatory power included stand age categorical variables, the frequency of precipitation on the day of *R*w measurements, and tree diameter at breast height (Table 2). Including those additional variables in our final best specification of the *R*w model improved the model fit to $R^2 = 0.82$.

3.2.2. Effect of Stand Age and Resulting Physiology

[39] Intersite differences in the *R*s-*T*s model, and thus, *R*s variability were observed between all four sites. In the initial analysis of observed data we used dummy variables to represent site differences. The estimated coefficients of all three of the site dummy variables were statistically significant (i.e., $P < 0.05$), and the magnitudes of their estimated coefficients were negative (i.e., -0.18, -0.10, and -0.34 for TP74, TP89, and TP02, respectively), suggesting that *R*s at the three younger stands was lower compared to TP39. However, in subsequent analysis, we found that two of the site variables could be replaced with site physiological variables. For example, when the thickness of the soil LFH horizon (LFH) was added into the model (i.e., equation 1 modified with dummy variables, as outlined in equations 2a–2c), the estimated coefficients of the dummy variables representing TP02 became insignificant, and the model did not converge. Similarly, the variable representing the carbon-to-nitrogen ratio of the LFH horizon and the dummy variable representing TP74 were mutually exclusive, if included together in the model, requiring one of the variables to be dropped.

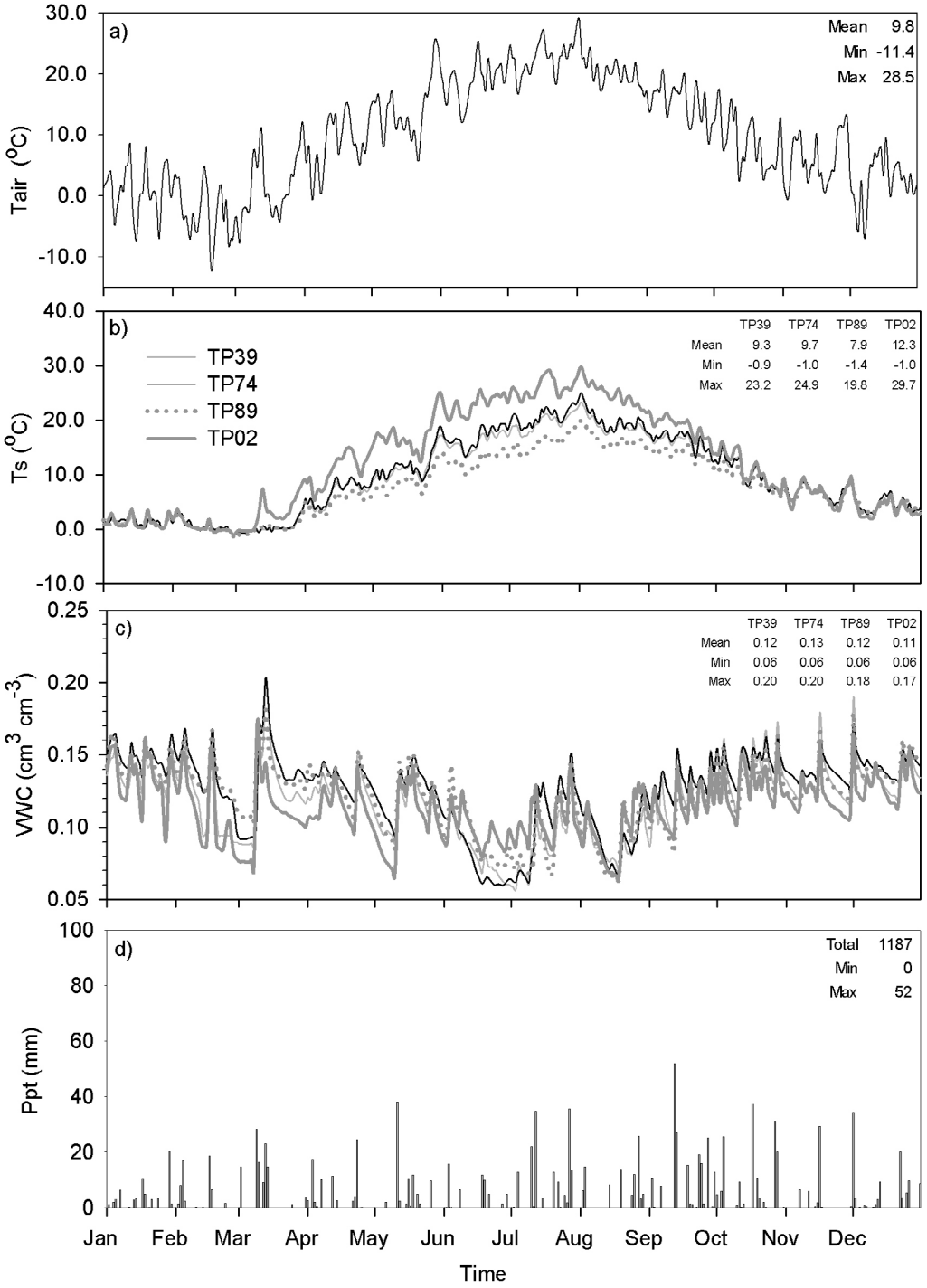

Figure 1. Comparison of climatic and edaphic conditions across Turkey Point sites in 2006. (a) Daily mean air temperature, *T*air, (b) daily mean soil temperature, *T*s (mean of all sensors in top 20 cm of mineral soil), (c) daily mean soil moisture content, VMC (mean of all sensors in top 20 cm of mineral soil), and (d) daily total precipitation, Ppt. Also listed in top right corner of each plot are the annual mean or total values, as well as the annual minimum and maximum values.

Therefore, we retained only LFH and CN in the final model and dropped the categorical variables for TP74 and TP02 (Tables 2). The model′s estimated R^2 remained unchanged when the dummy variables were replaced with the more physically meaningful variables.

[40] We also evaluated intersite differences in *R*f and found that, on per-leaf-area basis, there was no statistical difference in *R*f between the two oldest stands (TP39 and TP74) because the dummy variable representing TP74 was found to be statistically insignificant ($P > 0.05$) in the

Table 3. Estimated Coefficients of the Model Parameters in the Best Specification of the Gamma Models for Each Component Flux[a]

	*R*s			*R*f			*R*w		
Parameters	Estimated Coefficient	*t* Value	*P* Value	Estimated Coefficient	*t* Value	*P* Value	Estimated Coefficient	*t* Value	*P* Value
β_{01}	−90.57	−42.5	<.0001	−111.45	−5.9	<.0001	−71.02	−10.1	<.0001
β_1	−0.49	−34.9	<.0001	−0.40	−4.1	<.0001	−0.31	−7.7	<.0001
α	29.48	40.6	<.0001	33.20	5.5	<.0001	22.57	9.7	<.0001
β_{02}	−0.20	−9.5	<.0001	0.17	4.2	<.0001	0.93	11.2	<.0001
β_{03}				2.68	4.8	<.0001	1.22	13.5	<.0001
β_{12}				−0.03	−4.1	<.0001			
β_2	0.02	13.9	<.0001	−0.46	−9.3	<.0001	0.47	8.7	<.0001
β_3	0.12	7.2	<.0001	$4.8\text{x}10^{-4}$	2.5	0.0113	0.03	6.7	<.0001
β_4	0.14	12.9	<.0001	$7.1\text{x}10^{-3}$	4.2	<.0001			
β_5	−0.02	−9.3	<.0001						

[a]Also shown are the associated statistics: *t* and *P* values. See Table 2 for model equations.

model. In contrast, the dummy variables representing TP89 and TP02 were statistically significant, and their estimated coefficients were higher than the reference site (TP39). This suggested that *R*f at the youngest two stands, on per-leaf-area basis, was statistically different and higher from *R*f of the older stand (Table 3). However, unlike for the *R*s model, we did not find environmental or physiological variables to replace the dummy variables in the *R*f model.

[41] Intersite differences in *R*w were also important to consider because the dummy variables representing TP74 and TP89 were found to be statistically significant (Table 3). The estimated coefficients of the two variables were positive and implied that *R*w values, on per-sapwood-volume basis, at TP74 and TP89 were higher than those at TP39, with the highest rates at TP89. DBH and precipitation frequency also had a strong contribution to the model's R^2. Similar to the *R*f model, we were unable to find physiological or environmental factors that could statistically explain the intersite variability in *R*w. Therefore, the dummy variables were retained in the final *R*w model.

3.3. Contribution of Individual Component Fluxes to Ecosystem Respiration, *R*e

[42] Observed mean annual *R*s values were 2.2, 1.9, 1.8, and 1.9 μmol CO_2 m^{-2} s^{-1} for the TP39, TP74, TP89, and TP02 year-old stands, respectively, with ranges of 0.3–5.9, 0.3–4.5, 0.3–4.7, and 0.3–4.2 μmol CO_2 m^{-2} s^{-1}, respectively (Figures 2b–2e). Similarly, simulated mean annual *R*s values were 1.8, 1.5, 1.4, and 1.5 g C m^{-2} d^{-1} for the TP39, TP74, TP89, and TP02 sites, respectively (Figure 2a). While the magnitude of simulated *R*s was generally lower compared to observations, the temporal trend was well represented. Mean daily soil respiration was lowest during winter months and peaked in late July to early August (Figure 2a). Estimated annual *R*s values were 671 ± 33, 558 ± 35, 511 ± 36, and 539 ± 32 g C m^{-2} yr^{-1} for the TP39, TP74, TP89, and TP02 year-old stands, respectively. The highest annual *R*s value was observed at the oldest stand, TP39, and was different from the annual *R*s at the three youngest stands (Figure 5). In contrast, annual *R*s values among the three youngest stands of various ages were comparable (Figure 5).

[43] Observed annual mean foliar respiration, *R*f values were 1.6, 2.1, 2.5, and 2.9 μmol CO_2 (half-surface area of needles) m^{-2} s^{-1} at TP39, TP74, TP89, and TP02, respectively, with the corresponding *R*f ranges of 0.2–3.0, 0.9–3.3, 1.0–4.3, and 0.7–5.8 μmol CO_2 (half-surface area of needles) m^{-2} s^{-1}, respectively (Figures 3b–3e). We note that measurements at TP74 and TP89 were made only for 3 months of the year (June through August, n = 9), whereas measurements at TP39 and TP02 spanned over spring and autumn months as well (i.e., April through November). Therefore, the observed temperature range is smaller at TP74 and TP89 in Figures 3c and 3d. Observed *R*f rates decreased with increasing stand age, with the highest *R*f rates observed at TP02. However, the upscaled annual *R*f totals did not follow this age pattern and were 726 ± 182, 527 ± 132, 1203 ± 290, and 234 ± 33 g C m^{-2} yr^{-1} for the TP39, TP74, TP89, and TP02 year-old stands, respectively (Figures 3 and 5).

[44] Observed annual mean *R*w values were 38.1, 55.4, and 81.1 μmol CO_2 (sapwood volume) m^{-3} s^{-1} at the TP39, TP74, and TP89 year-old stands, respectively, with the respective *R*w ranges of 3.4–151.3, 4.8–162.6, and 5.4–187.5 μmol CO_2 (sapwood volume) m^{-3} s^{-1} (Figures 4b–4d). The course of temporal variability in *R*w followed closely that of air temperature variability, given that the bole temperatures were highly correlated with *T*a (results not shown). Annual total values of *R*w were 129 ± 13, 193 ± 14, 271 ± 14, and 0.7 ± 0.04 g C m^{-2} yr^{-1} for TP39, TP74, TP89, and TP02, respectively (Figures 3 and 5). Unlike for *R*f and *R*s, *R*w values, both, on per-sapwood-volume and ground-area basis, followed a distinct linear age-related pattern across the three oldest TPFS stands, i.e., *R*w decreased with increasing stand age (Figures 4 and 5).

[45] Based on upscaled chamber measurements, annual total *R*e values were estimated to be 1526 ± 137, 1278 ± 137, 1985 ± 293, and 773 ± 46 g C m^{-2} yr^{-1} at TP39, TP74, TP89, and TP02, respectively (Figure 5). Annual totals at the two oldest stands, TP39 and TP74, were comparable, that of the TP89 stand was the highest of all four stands, while that of the youngest TP02 stand was the lowest of all. At the TP02, *R*s accounted for 70% of *R*e, with *R*f accounting for the remaining 30%. *R*w was minimal (0.1%) at that site. This was in contrast to the TP89 stand, where *R*f accounted for the majority of the annual *R*e (60%), with *R*s accounting for an additional 26% and *R*w for 14%. At the two oldest stands, TP39 and TP74, the contributions of *R*s to annual *R*e were comparable (i.e., 44% each), whereas the contribution of *R*f to *R*e at TP39 was higher than that at TP74 (i.e., 48% versus 41%, respectively). In contrast, *R*w contribution at TP74 was higher compared to TP39 (i.e.,

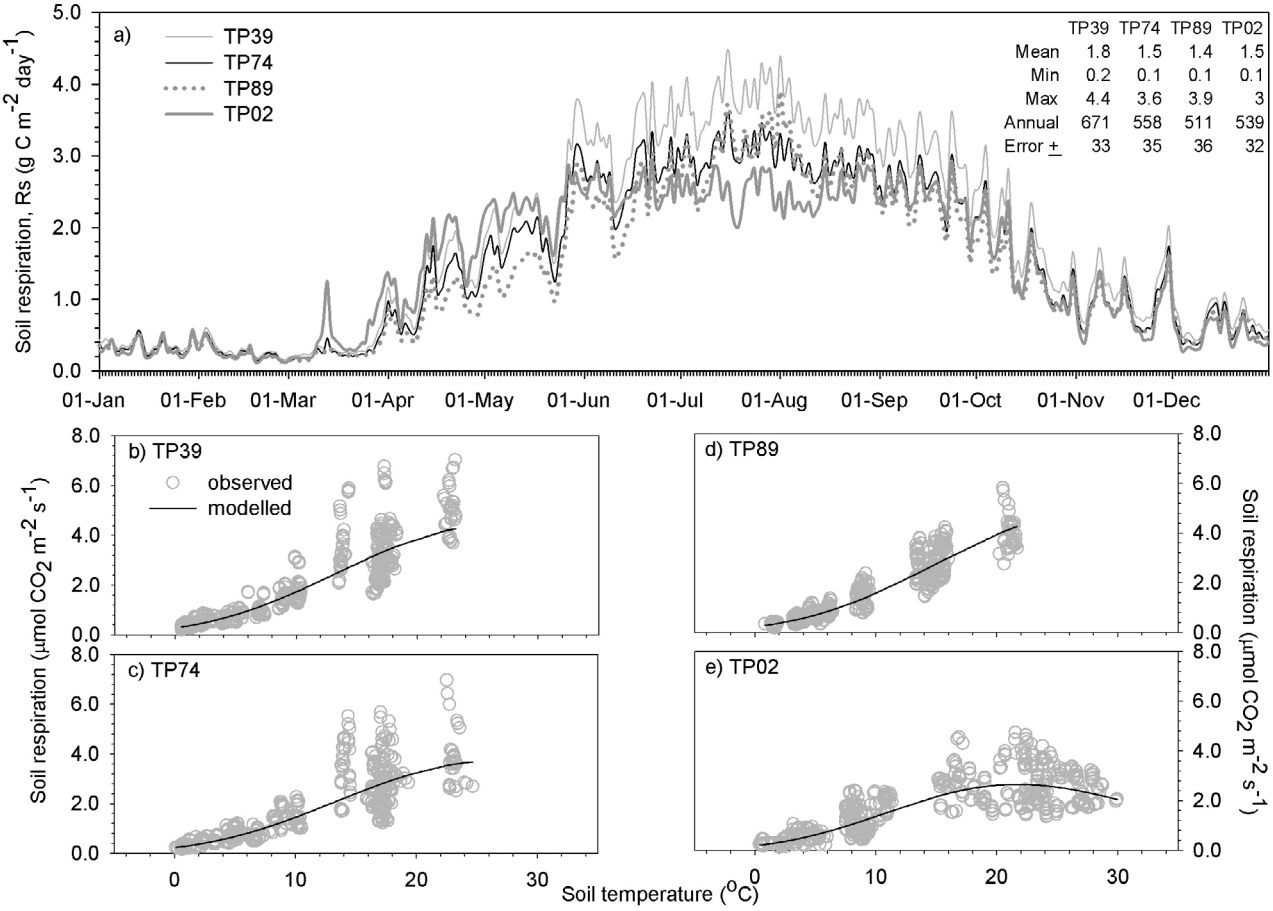

Figure 2. Comparison of (a) simulated daily mean soil respiration *R*s in g C m^{-2}, across Turkey Point sites in 2006, and (b–e) relationships between observed *R*s (μmol CO_2 m^{-2} s^{-1}) versus soil temperature (*T*s) across all four sites. Symbols represent measured values, whereas lines represent simulations using the *T*s -only Gamma model. In the top right corner of Figure 2a, annual mean, minimum, and maximum simulated *R*s values are listed as well as total annual emissions with their estimated errors in g C m^{-2}.

15% versus 8%, respectively). The relative percent contribution of the individual *R*e components to total annual *R*e was variable across all four stands throughout the year (Figure 6). During the growing season, *R*f dominated *R*e, whereas in winter months, *R*s dominated *R*e. Even at TP02, in August, *R*s and *R*f were comparable in their contribution to *R*e (Figure 6), highlighting the importance of foliar respiration in the carbon cycle of young to mature afforested stands.

3.4. Comparison of *R*e Derived by Chamber Versus Eddy Covariance Methods

[46] On a daily scale, chamber-based estimates of *R*e overestimated the eddy covariance, EC-based *R*e estimates (*R*e_ec) from April to November across all four stands (Figure 7), although *R*e from both methods was highly correlated (i.e., for 1:1 relationships, R^2 = 0.94–0.96, plots not shown). The high correlation could be in part due to temperature being used as the main predictor of simulated fluxes in both methods. At TP02, upscaled chamber estimates of *R*e better matched observed nighttime NEE values in July (Figure 7d). Annual total *R*e_ec values were 1293, 751, 1678 and 569 g C m^{-2} yr^{-1} at the TP39, TP74, TP89 and TP02, respectively. At all four stands, *R*e values were higher than *R*e_ec by 18% at TP39 and TP89, by 70% at TP74, and 36%, at TP02.

4. Discussion

4.1. Meteorology and Site Microclimate

[47] The study year was relatively warmer and wetter compared to the norm for the area, and therefore, it is possible that some of the discrepancy between estimated *R*e values at our sites and those reported in relevant literature could be due to this more favorable climate for growth at our sites. The estimated component fluxes may have been higher this year because variability in both air temperature and precipitation was included in model simulations of individual component fluxes (Table 2). Despite that, our results support the idea that in young afforested stands, the lack of forest floor accumulation and canopy cover lead to a stronger coupling between the soil and the atmosphere. For example, at TP02, the site without LFH accumulation and an open canopy, soil temperatures reached the highest values. At TP02, *T*s was more strongly coupled to *T*a compared to the older three stands. In contrast, TP89 had the

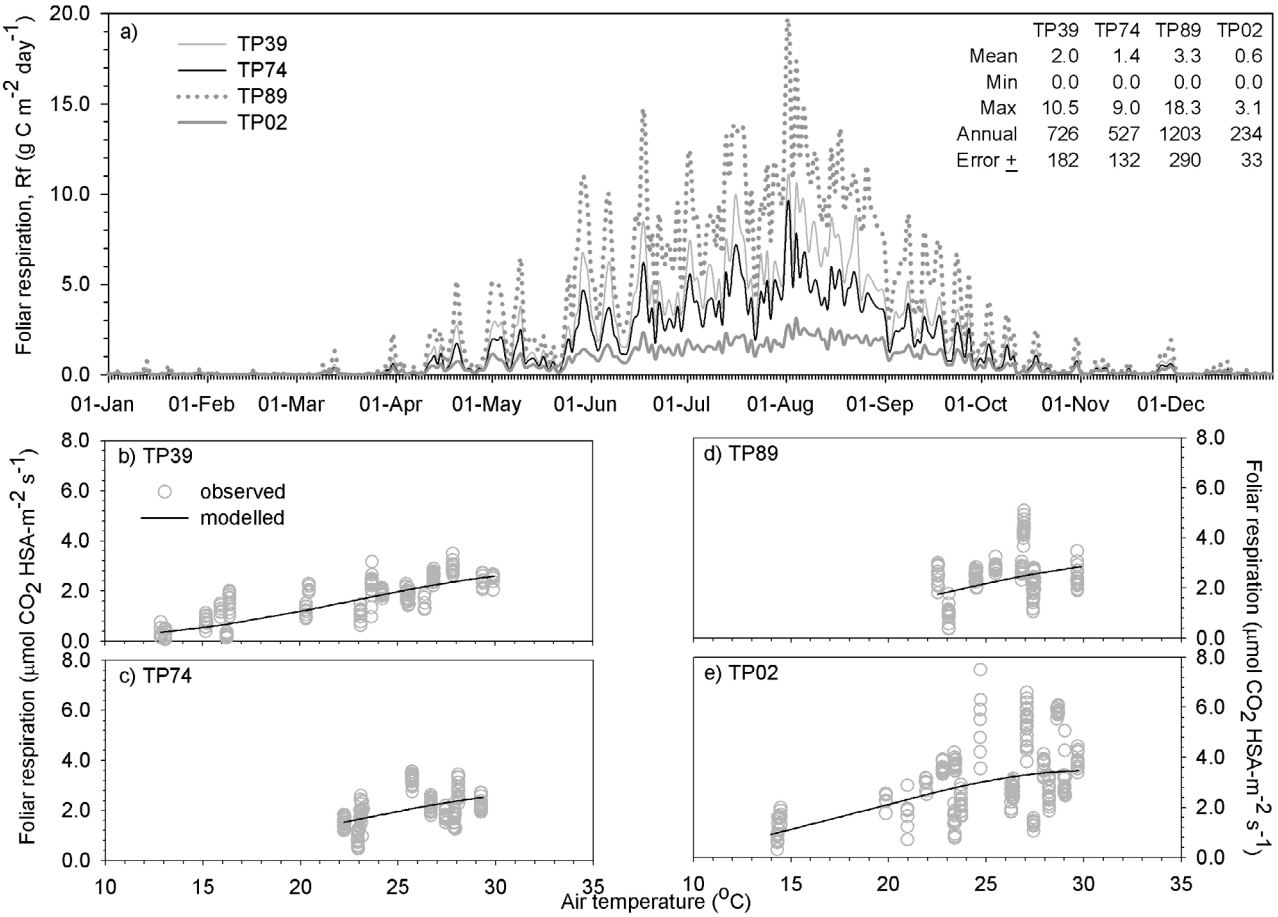

Figure 3. Comparison of (a) simulated daily mean foliar respiration (*R*f) in g C m^{-2}, across Turkey Point sites during 2006, and (b–e) relationships between observed *R*f (μmol CO_2 (half-needle surface area in m^{-2}) s^{-1}) versus air temperature (*T*a) across all four sites. Symbols represent measured values, whereas lines represent simulations using the *T*s-only Gamma model. In the top right corner of Figure 3a, annual mean, minimum, and maximum simulated *R*f values are listed as well as total annual emissions with their estimated errors in g C m^{-2}.

highest LAI and relatively thick litter layer accumulation, which resulted in the lowest *T*s among sites and highest time lag between *T*s and *T*a. Therefore, the differences in the sites′ microclimates that resulted from age-related differences in stand physiology contributed to the variability in observed respiration fluxes.

4.2. Environmental and Physiological Controls on Respiration

[48] Because of the relatively open canopy and lack of litter layer, *R*s increased about 1 month earlier in spring at TP02 as compared to three older stands (Figure 2, March–April). A similar phenomenon was reported previously by *Noormets et al.* [2007] but for *R*e. In our study, seasonal dynamics in *R*e were generally dominated by *R*f across our stands.

[49] The highest annual *R*f was obtained at TP89, the site with the highest LAI, whereas the lowest annual *R*f was obtained at TP02, the site with the lowest LAI (Table 1). Estimated annual *R*f values, on a per ground area basis, for all but the youngest Turkey Point stand (TP02), were much higher compared to those reported in similar studies in the literature. For example, *Tang et al.* [2008] reported *R*f values of 69–121 g C m^{-2} yr^{-1}, whereas *Law et al.* [1999] reported 157 g C m^{-2} yr^{-1} from their upscaling studies in old-growth forests. Similarly, *Gaumont-Guay et al.* [2006] reported total estimated *R*f in the range of 173 ± 14 to 243 ± 21 g C m^{-2} yr^{-1} in their study of component fluxes of an 81-year-old boreal aspen forest. However, our measured *R*f rates, on per leaf area basis, were close to the range and seasonality reported by *Cooper et al.* [2006] in a mixed conifer forest in Washington, USA (0–4.6 μmol CO_2 m^{-2} s^{-1}), which attained maximum values in June and minimum in December. Therefore, intersite variability of upscaled *R*f values among our stands, as well as between our stands and those reported in literature, was driven by intersite differences in leaf area indices.

[50] At TP02, very low *R*w was due to the low sapwood volume per hectare in this young seedling site (Table 1). Otherwise, across our sites the range of observed live woody tissue respiration was larger compared to *R*w values reported in the literature but comparable to literature values once upscaled on per ground area basis. For example, *Tang et al.* [2008] reported *R*w values of 4–40 μmol CO_2 (sapwood

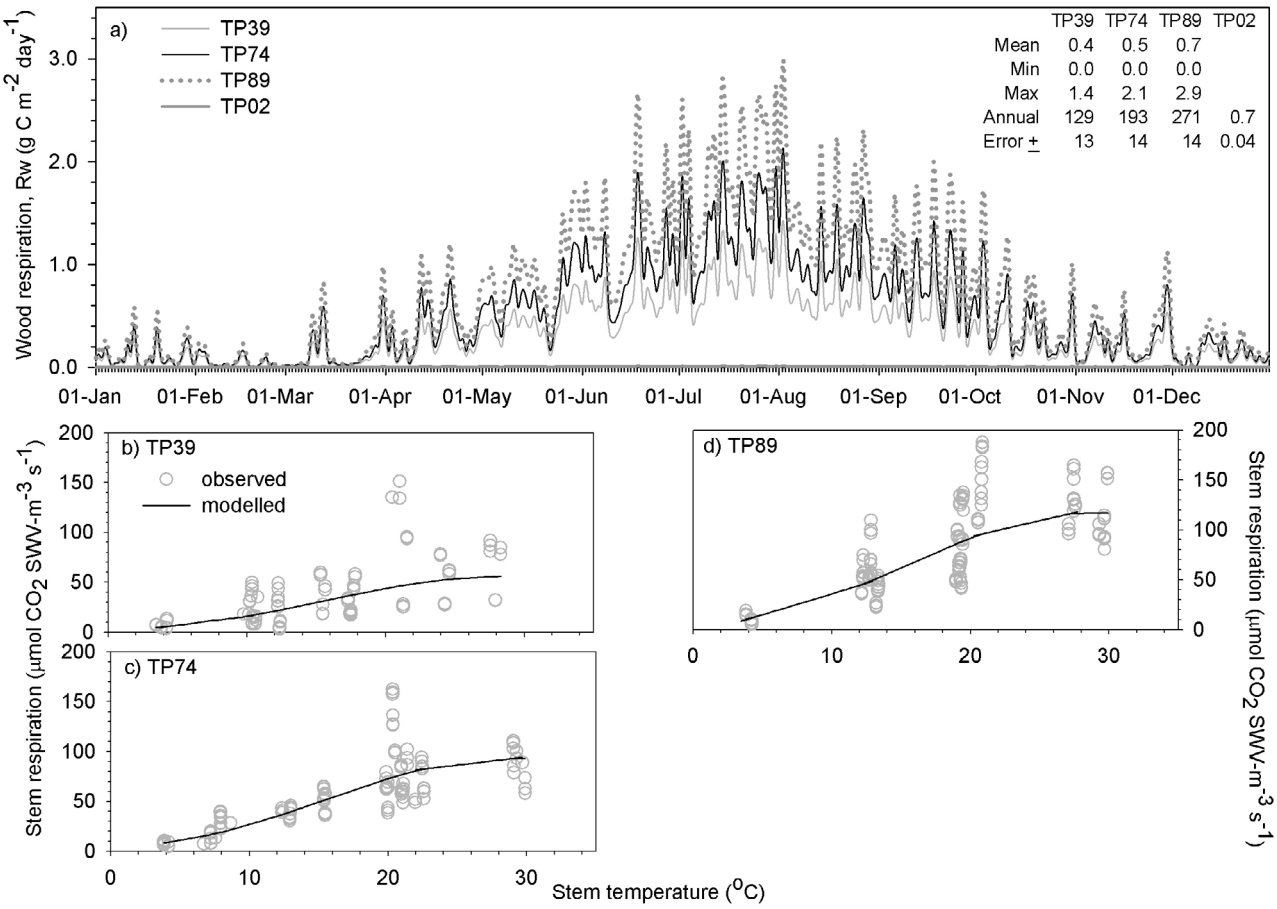

Figure 4. Comparison of (a) simulated daily mean woody tissue respiration (*R*w; which included both branch and stem respiration) in g C m^{-2}, across Turkey Point sites during 2006, and (b-d) the relationships between observed *R*w (μmol CO_2 (sapwood volume of stem in m^{-3}) s^{-1}) versus tree bole temperature (*T*b) across all four sites. Symbols represent measured values, whereas lines represent simulations using the *T*s-only Gamma model. In the top right corner of Figure 4a, annual mean, minimum, and maximum simulated *R*w values are listed, as well as total annual emissions with their estimated errors in g C m^{-2}.

volume) m^{-3} s^{-1} in the mixed-wood forest in Michigan, USA, but 130–209 g C per m^2 yr^{-1}. Similarly, *Law et al.* [1999] reported *R*w of 2.5–19.5 μmol CO_2 (sapwood volume) m^{-3} s^{-1} in their ponderosa pine forest in Oregon, USA, and 54 g C per m^2 yr^{-1}. *Griffis et al.* [2004] reported stem respiration of 155–198 g C per m^2 yr^{-1} in their 74-year-old boreal aspen forest. The differences between Turkey Point stands and literature values of *R*w could be due to physiological differences, such as differences in sapwood volume per ground area between our sites and those in literature. High sapwood production, and consequently high *R*w, at our sites may be partly caused by greater water availability in deeper soil layer (~1 m depth) at TP89. *Peichl et al.* [2010] discussed the unlimited/continuous soil water access for trees at TP89, which allows those trees to have exceptional amounts of productivity (both foliar, i.e., LAI, and sapwood), compared to the other three TPFS stands. Indeed, foliar biomass across our sites was highest for TP89, suggesting high productivity (Table 1) and estimated sapwood growth at DBH was also highest at TP89 in 2006 (i.e., 9.9 cm^2 at TP89, versus 6.2 cm^2 at TP39 and 3.3 cm^2 at TP74, unpublished data).

[51] Other reasons for the intersite differences in CO_2 emissions among our stands, as well as among our sites and those reported in literature, could be differences in site quality. For example, intersite variability in observed *R*f values (on per HSA of needles) among our stands was likely due to intersite variability in foliar nitrogen content, with the highest foliar N and *R*f values observed at TP02 (Figure 3 and Table 1). Foliar gas exchange has been shown to relate strongly and positively to foliar nitrogen content [*Dang et al.*, 1997; *Vose and Ryan*, 2002]. The amount of soil nutrients such as phosphorus, magnesium, and potassium in the surface soils at TP89 support the idea that site quality at TP89 may have been better suited for tree growth compared to TP39 or TP74. *Peichl et al.* [2010] discussed in more detail the effects of site quality on intersite differences in ecosystem respiration across TPFS. Finally, the generally higher and more spatially variable amounts of soil nutrients at the younger stands (Table 1) are reflective of the sites′

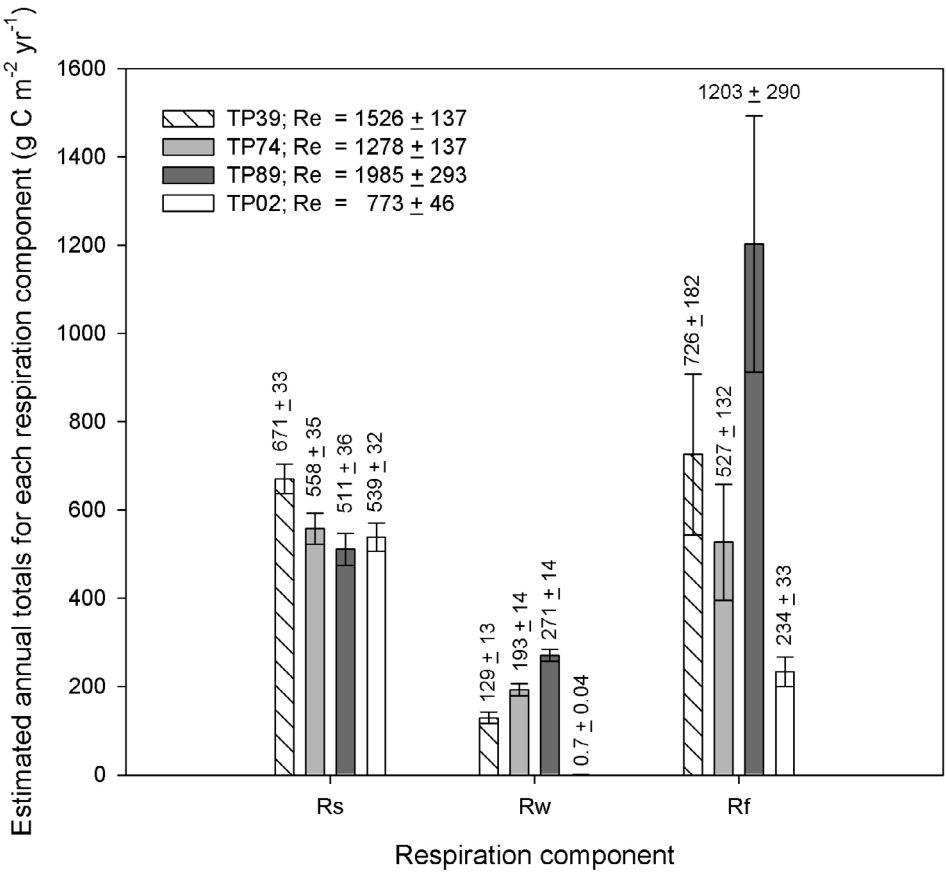

Figure 5. Intersite comparison of annual totals of the three major ecosystem respiration components, i.e., total soil (*R*s), woody tissue (*R*w), and foliar (*R*f) respiration, in g C m^{-2} yr^{-1}. Also included are estimated annual totals of ecosystem respiration (*R*e) in the legend. Estimated errors on each total are shown as ± error bars and numerically.

past agricultural land use, suggesting that past land use history is an important factor to consider when studying carbon dynamics of young afforested stands.

4.3. Contribution of Individual Component Fluxes to Ecosystem Respiration, *R*e

[52] Annual *R*e values across our sites (Figure 7) were higher than literature-reported values, especially for TP89. For example, *Law et al.* [1999] reported *R*e of 894 g C per m^2 yr^{-1} from upscaled chamber measurements in their old-growth ponderosa pine forest in Oregon, whereas *Tang et al.* [2008] reported a range of 600–742 g C per m^2 yr^{-1} in their old-growth mixedwood site in Michigan, USA. For comparison, *Gaumont-Guay et al.* [2006] reported upscaled chamber-based *R*e of 1190 g C per m^2 yr^{-1} for an 81-year-old aspen stand in Saskatchewan, Canada. Differences in LAI and stand age are the likely reasons for the discrepancy.

[53] In a recent study, *Lindroth et al.* [2008] have shown that intersite differences in *R*e across a number of coniferous forests in northern Europe were driven first by differences in LAI and second by differences in stand age. The generally high LAI at our Turkey Point sites was attributed to high values of white pine needle clumping [*Chen et al.*, 2006], which could be species specific. Maximum LAI values across our three older stands varied from 5.9 to 12.8, with an estimated annual mean of 3.4–7.4 (Table 1). In contrast, LAI of the stands studied by *Tang et al.* [2008] averaged 3.8–4.1, whereas that of the ponderosa pine stand studied by *Law et al.* [1999] was only 1.5. The highest LAI at TP89 may have been due to more favorable soil water availability and nutrient conditions compared to the two older stands and/or because of the fact that TP89 was in an active stage of growth for white pine species.

[54] *Noormets et al.* [2007] studied the effect of stand age on total ecosystem carbon fluxes in managed forests (3 to 65 years old) in the Great Lakes region and reported higher *R*e in younger stands compared to older ones, explaining that the difference was due in part to the inherent greater biological activity of younger stands. Results presented in this study suggest that on annual basis, foliar respiration dominated ecosystem respiration at our older (17- to 67-year-old) stands, which was in contrast to the more widely reported dominance of *R*s on *R*e in forested ecosystems [*Bolstad et al.*, 2004; *Law et al.*, 1999; *Gaumont-Guay et al.*, 2006; *Tang et al.*, 2008; *Zha et al.*, 2009]. The unusually high *R*f in our study, especially for the 17-year-old stand, may be due to the young age of the stand and its inherent high productivity. Recent studies have suggested a strong positive link between CO_2 emissions in forests and their primary productivity, whereby increased productivity

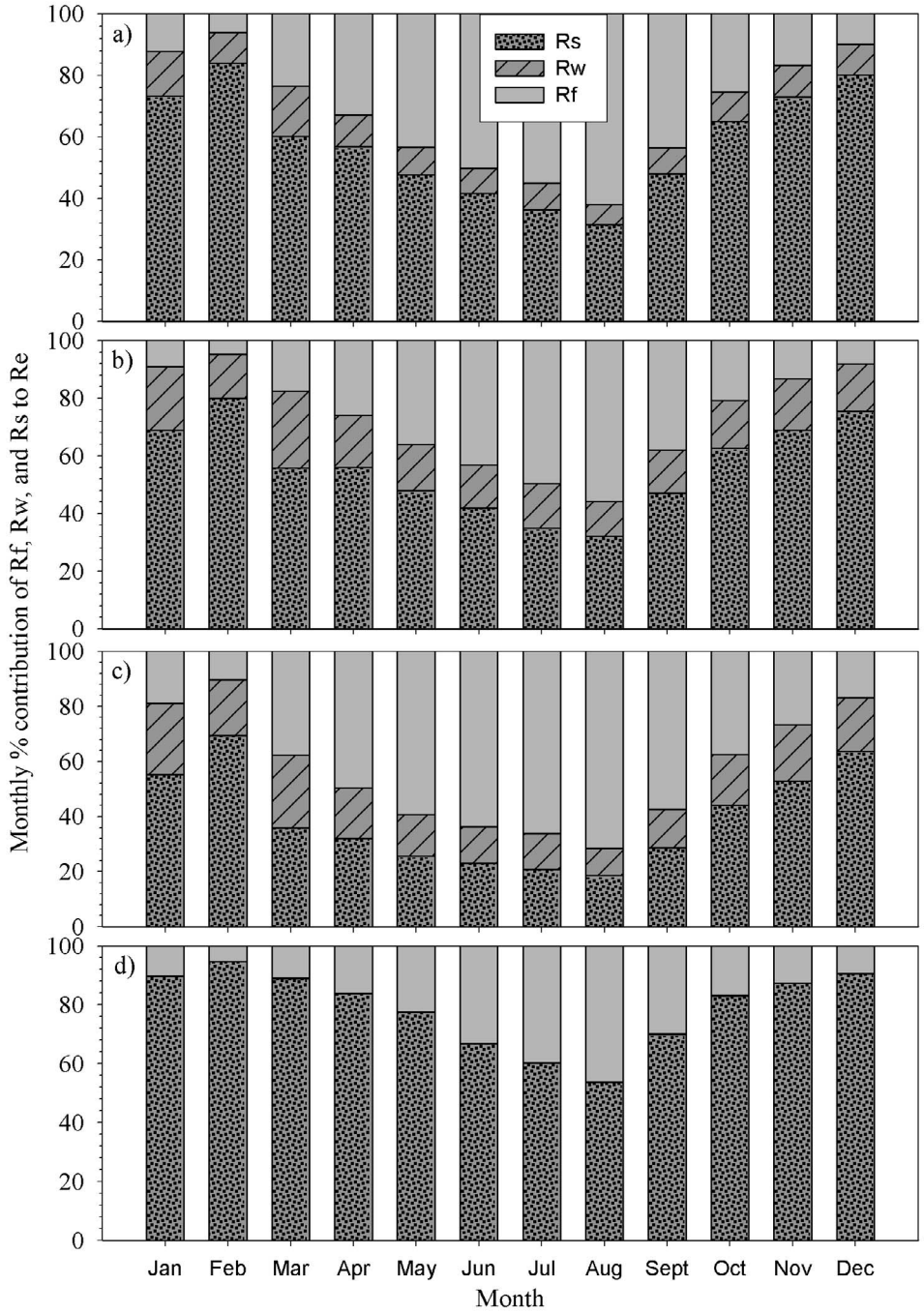

Figure 6. Comparison of percentage-relative contribution of monthly soil respiration (*R*s), woody tissue respiration (*R*w), and foliage respiration (*R*f) to total monthly ecosystem respiration at (a) TP39, (b) TP74, (c) TP89, and (d) TP02 site.

leads to increased respiration [*Hibbard et al.*, 2005; *Litton et al.*, 2007]. Furthermore, there is increasing evidence that across different forest biomes, productivity tends to increase with forest age up to an age of about 120 years [*Pregitzer and Euskirchen*, 2004; *Noormets et al.*, 2007; *Gough et al.*, 2008], with peak production occurring around 11–30 years in temperate forests [*Pregitzer and Euskirchen*, 2004]. *Lancaster and Leak* [1978] have shown that white pine productivity tends to peak around the age of 15 years, which is close to the age of TP89, the site with the highest *R*e.

4.4. Comparison of *R*e Derived by Chamber Versus Eddy Covariance Technique

[55] Our results agree with literature studies that generally report higher values of chamber-estimated *R*e as compared to eddy covariance-based estimates (*R*e_ec). For example,

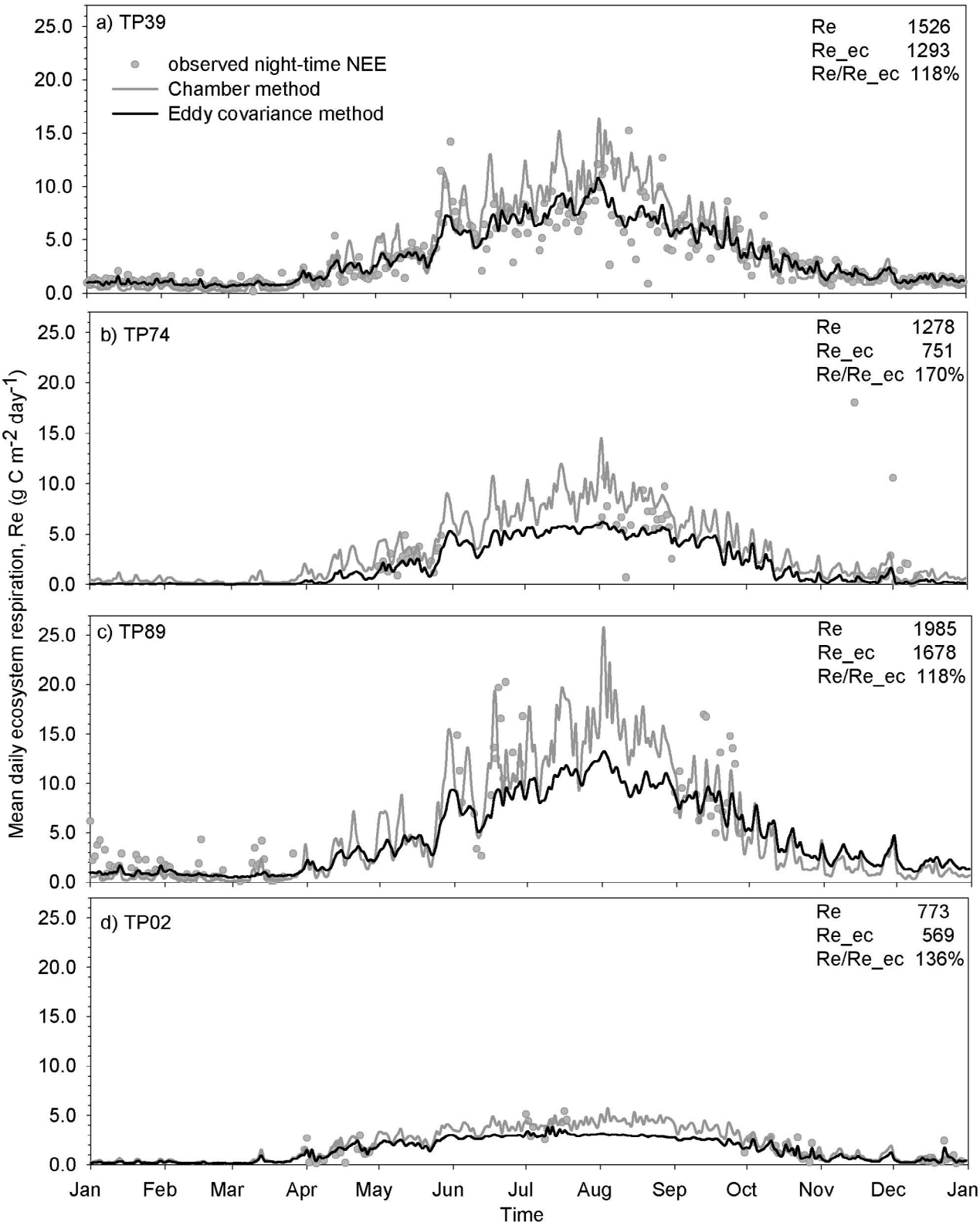

Figure 7. Comparison of simulated mean daily ecosystem respiration estimates using the models developed by the chamber-based (*R*e) and by the eddy covariance (*R*e_ec) measurements. Observed values of daily mean nighttime net ecosystem exchanges (NEEs) are also shown. (a) TP39, (b) TP74, (c) TP89, and (d) TP02. In the top right corner of each frame, annual totals estimated from each method in g C m^{-2} yr^{-1} and their ratios are also given.

Griffis et al. [2004] reported chamber-based *R*e to be higher than *R*e_ec by 20%–37% at the boreal aspen forest in Canada and *Gaumont-Guay et al.* [2006] reported chamber-based *R*e to be higher by 25% at the same aspen site. Similarly, *Lavigne et al.* [1997] reported chamber-based *R*e to be higher by 20%–40% compared to *R*e_ec at the six boreal forest sites in Canada. *Law et al.* [1999] reported 50% higher chamber-based *R*e estimates compared to *R*e_ec in their study. In contrast, *Tang et al.* [2008] reported only a 2% difference between the two methods but with chamber-based *R*e values being higher. Our percent differences (18%–70% on average) were within those reported in the literature.

[56] The discrepancy between chamber- and eddy covariance-based estimates could be due to numerous reasons and are difficult to account for. For example, the eddy covariance technique may underestimate emissions during nighttime because of low turbulence conditions. For a more detailed account of possible causes of *R*e_ec underestimation, see a recent review by *Aubinet* [2008]. Alternatively, it may be possible that what was measured by the chambers was not within or representative of the overall tower footprint, thus causing discrepancies between the resulting estimated *R*e values [*Lavigne et al.*, 1997]. There could also be a number of errors in chamber methods, related to inadequate estimates of biological indices, such as LAI (i.e., if too few measurements were taken during the year to account for seasonality in LAI as well as vertical difference in *R*f within the canopy) and sapwood volume (i.e., compressing the tree core, when coring the tree to measure sapwood width in a stem sample) used for upscaling. *Lavigne et al.* [1997] discusses in more detail some of the challenges in upscaling chamber-based estimates of *R*e to those derived with the eddy covariance technique.

[57] The continued observed discrepancy between eddy covariance estimates of *R*e and chamber-based estimates, across a number of studies in different ecosystems, suggests that caution should be taken when one tries to estimate the relative percent contribution of *R*s to *R*e at a site by using chamber-based estimates of *R*s and eddy covariance-based estimates for *R*e. Conclusions about the ecosystem′s carbon cycle derived from such calculations could be flawed. On the basis of our study, we would caution against such a practice, until differences between the two methods have been resolved, or unless the researchers can demonstrate close agreement between *R*e estimated by both methods for their sites. Otherwise, the relative contribution of *R*s to *R*e for a given site could be grossly overestimated.

5. Conclusions

[58] We measured CO_2 emissions from soil (*R*s), foliage (*R*f), and live woody tissue (*R*w) in four temperate white pine (*Pinus strobus* L.) ecosystems aged 67, 32, 17, and 4 years old at the time of the study. Temperature was the dominant environmental factor driving temporal variability of all three individual components of ecosystem respiration, *R*e. However, other environmental and physiological factors also showed statistical significance in their control on inter-site and temporal variability in *R*e.

[59] Overall, our results suggest that young actively growing stands may have CO_2 emissions comparable to mature stands and that in such stands *R*f may dominate *R*e, especially during the growing season. Intersite variability in CO_2 emissions was attributed to differences in stand physiological characteristics, such as the presence of the LFH horizon, canopy cover, foliar, and soil nutrient status. These differences in stand characteristics were reflective of site quality and stand age and highlight the importance of considering, both, stand age, and the knowledge of past land use history, when assessing carbon budgets of planted or afforested ecosystems. However, more chronosequence studies are required to confirm this trend because we were unable to separate differences in site quality due to our limited data set. Improved site quality, in terms of soil water availability and nutrients, may overshadow or confine any age-related trends.

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